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A review of the southern African genus *Tongamya* (Diptera: Asiloidea: Mydidae: Megascelinae), with a molecular assessment of the phylogenetic placement of *Tongamya* and the Megascelinae

by

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ABSTRACT

This paper both tests the morphologically based cladistic appraisal of the Apioceridae proposed by Yeates & Irwin (1996) using the 28S ribosomal RNA gene and reviews the systematic status and biology of *Tongamya* and the subfamily Megascelinae to which it belongs. Yeates & Irwin (1996) concluded that the subfamilies Rhaphiomidinae and Megascelinae, both formerly placed within the Apioceridae, were separate basal lineages of the family Mydidae. The 28S rDNA evidence presented here confirms the sister group relationship of *Tongamya* and *Megascelus*, their retention in the subfamily Megascelinae, the removal of that subfamily from the Apioceridae and its placement within the family Mydidae. New material and field observations of flies belonging to the genus *Tongamya* enable us to expand the known range of *Tongamya miranda*, describe a second species, *Tongamya stuckenbergi* sp. n., better diagnose *Tongamya* and its two included species, and expand on the habitat and flight behaviour of this remarkable and rarely encountered genus of flies.

INTRODUCTION

In 1996, a cladistic appraisal of the dipterous family Apioceridae, based on morphological features, revealed that the taxa comprising the Rhaphiomidinae (genus *Rhaphiomidas* Osten Sacken, 1877) and Megascelinae (genera *Neorhaphiomidas* Norris, 1936; *Megascelus* Philippi, 1865; and *Tongamya* Stuckenberg, 1966) were paraphyletic with respect to the rest of the Apioceridae (Yeates & Irwin 1996). This appraisal concluded that Rhaphiomidinae and Megascelinae, both formerly placed within the Apioceridae (Norris 1936; Cazier 1965; Carrera & d'Andretta 1948; Stuckenberg 1980; Peterson 1981), were separate basal lineages of the closely related family Mydidae. The subsequent revised classification left a monophyletic family, Apioceridae, containing the single, widespread genus, *Apiocera* Westwood, 1835, with four monophyletic subgenera. This appraisal further concluded that, within the Megascelinae, *Neorhaphiomidas* and *Megascelus* are sister genera, and *Tongamya* forms a sister-group to *Neorhaphiomidas* plus *Megascelus* (Yeates & Irwin 1996; see cladogram Fig. 64). In this study, we assess the morphology-based phylogenetic relationships hypothesised for Apioceridae (*Apiocera*), Rhaphiomidinae (*Rhaphiomidas)*, Megascelinae (*Tongamya*, *Megascelu*s), and the remainder of the Mydidae (several genera) using nucleotide data from the 28S ribosomal RNA gene (=28S rDNA).

Even though most contain several species, the genera in the subfamilies Rhaphiomydinae and Megascelinae have rather restricted geographical ranges. The rhaphiomidine genus *Rhaphiomidas* contains 19 known species and a number of subspecies, all endemic to the southwestern United States and northwestern Mexico (Cazier 1985). Of the megasceline genera, *Neoraphiomidas* includes seven species, six in Western Australia and one in South Australia (Daniels 1989); *Megascelus* includes five species (Artigas 1970 1973; Bernardi 1975), all endemic to central Chile, spanning the area from Coquimbo Province southward to and including Malleco Province; and the genus *Tongamya* forms an exception in that it is currently known from a single species, *T. miranda* Stuckenberg, 1966, albeit with an extremely narrow geographic range, represented in published museum holdings by a handful of specimens collected in KwaZulu-Natal, South Africa (Stuckenberg 1966 1980; Irwin & Stuckenberg 1972).

Acquisitions by the Natal Museum, Pietermaritzburg, South Africa; the National Museum, Windhoek, Namibia; the Transvaal Museum, Pretoria, South Africa; together with a recent collecting expedition that one of us (MEI) led to Namibia have brought to light additional specimens of *Tongamya*. This material plus observations of these flies while in Namibia enable us to expand the known range of *Tongamya miranda*, describe a second species of that genus, better diagnose the genus, and expand on the habitat and flight behaviour of this remarkable and rarely encountered genus of flies.

METHODS

Processing, examining, illustrating, and observing specimens

Specimens of *Tongamya* collected by us were hand-netted in Namibia or South Africa and either placed immediately in 95% ethanol (e.g., *MEI 089484*) or pinned the evening of the day they were collected. Similarly, specimens for the molecular study, including apiocerids, mydids and megascelines, were preserved in 95% ethanol and refrigerated until used in molecular studies. Material used for morphological and descriptive aspects of this study was viewed under both Wild M5 dissecting and Zeiss compound microscopes. To prepare specimens for observing detailed features of mouthparts, antennae, and internal male and female genitalia, those structures were removed from the body of the fly, placed in room temperature 10% KOH overnight, rinsed in deionised water for ten minutes, placed in 70% and then 95% ethanol, and finally into glycerin, where the parts could be teased apart and the extraneous material removed. For the female genitalia, an extra step was taken. After the abdomen had been moved to 95% ethanol, it was dissected by teasing apart the tergal and sternal halves along the pleural membrane using two fine forceps. A drop of solution containing chlorozol black dissolved in 95% ethanol was then placed directly on the part of the dissected abdomen that contained the internal structures of the genitalia and allowed to stain the non-sclerotised epidermal organs for 15–20 seconds, after which the structure was rinsed in 95% ethanol and placed in glycerin for study. It was noted that upon placing the structure in glycerin, the thin-walled sacs partially or fully collapsed. A sketch was made of the expanded sacs before they were taken from the 95% ethanol to the glycerin, which allowed a more accurate description and drawing of these parts before collapse. Morphological features were named in accordance with McAlpine (1981). Female terminalia features were named in accordance with Irwin (1976) and Winterton *et al.* (1999). The homology of the male hypandrium was uncertain, as discussed in the text.

A drawing tube (*camera lucida*) attached to the dissecting and compound microscopes was used to make rough sketches of the diagnostic characters herein illustrated. These sketches were scanned into Adobe Photoshop® with an Epson® Expression® 800 scanner where they were enhanced and rendered into finished drawings by Jill Marie Mulett, our scientific illustrator (see acknowledgements) using a combination of Adobe

Illustrator® and Photoshop® with a Wacom® Intuos® graphics tablet and on an Apple® Power Mac™ G4. The habitus drwaings were scanned from original carbon dust renderings on clayboard.

MEI observed the flight behaviour of the few male specimens of *Tongamya stuckenbergi* that were taken in the Kalahari Desert of Namibia, and of *Megascelus albovillosus* collected in Chile. These traits are noted below.

Specimen numbers and database

All specimens referred to in this paper have been assigned unique numbers to facilitate the association of data through a database. The number consists of a three letter prefix plus a six-digit numeral. The prefix letters refer to the collection where the specimens were assigned unique numbers; the default prefix (*MEI*) is that provided by us when numbers were not preassigned to material from other collections. In the case of pinned specimens, the default number appears below the specimen on a yellow label bearing the following words: THEREVIDAE / M. E. IRWIN / SPECIMEN #. In the case of liquid-preserved material, a white label with the same information is included in the specimen vial. Numbers referring to specimens are to be found throughout the text (in parenthetical *italics*) to associate label data with loan, taxonomic, nomenclatural, ecological, behavioural and other information. These numbers and associated data have been entered into a data management system called Mandala (Kampmeier & Irwin 1998) created with FileMaker® Pro software. The Mandala Therevidae database is searchable via the Internet (Kampmeier 2000).

Museum and collection acronyms

Specimens used in this study were borrowed from or are being deposited with the following collections and museums.

BMNH	The Natural History Museum, London, England
CASC	California Academy of Sciences, San Francisco, USA
MEIC	Michael E. Irwin Collection, University of Illinois, USA (for eventual deposition with CASC)
MRAC	Musée Royal de l'Afrique Centrale, Tervuren, Belgium
NCSU	Brian M. Wiegmann Collection at North Carolina State University, USA (GenBank numbers associated with these specimens in Table 1)
NMSA	Natal Museum, Pietermaritzburg, South Africa
SMWN	Namibian National Insect Collection, State Museum, Windhoek
TMSA	Transvaal Museum, Pretoria, South Africa

Specimens examined

Specimens of *Tongamya* and others used in the molecular and morphological aspects of this study are recorded in a format similar to that presented in Irwin (1983). More detailed information on the specimens examined in this study can be found on an internet interactive database (Kampmeier 2000).

Molecular methods and phylogenetic analysis

The 16 species included in the molecular phylogenetic analysis were assigned unique MEI numbers and are listed below with associated collection information and in Table

1 listed in taxonomic hierarchy with MEI specimen numbers and GenBank accession numbers. Two species of Therevidae, *Ruppellia basalis* (*MEI 089480*) and *Anabarhynchus tristis* (*MEI 053735*), and a scenopinid, *Stenomphrale teutankhameni* (*MEI 029570*), were used as outgroups. Total genomic nucleic acids were extracted using the guanidinium isothiocyanate homogenisation protocol of Chirgwin *et al.* (1979) (after Cho *et al.* 1995). A 1.2 kbp fragment of the 28S rDNA was amplified in two segments using primers from Hamby *et al.* (1988) modified to match the published sequence for the dipteran, *Drosophila melanogaster* (GenBank Accession #M21017, Tautz *et al.* 1987) (Yang *et al.* 2000). Primers rc28H and 28K amplify an approximately 750 bp fragment (5982–6739 in *D. melanogaster*), and primers rc28Q and 28Z amplify an overlapping approximately 850 bp fragment (6385–7220 in *D. melanogaster*). Internal primers 28Q and rc28X were used in cycle sequencing reactions for some templates (Yang *et al.* 2000). PCR amplifications were carried out using standard 3-step PCR with 50ºC annealing temperature and 30 cycles.

TABLE 1

Taxa sampled for sequencing.

Taxon	Source	Collection ID	GenBank ACC #
Outgroups			
Family Scenopinidae			
Stenomphrale teutankhameni	Israel	MEI 029578	AF147824
Family Therevidae			
Ruppellia basalis	Namibia	MEI 089480	AF147833
Anabarhynchus tristis	Australia	MEI 053735	AF147847
Ingroup			
Family Apioceridae			
Apiocera (Anypenus) philippi	Chile	MEI 108205	AF266252
Apiocera (Apiocera) sp. #1	Australia	MEI 108212	AF266247
Apiocera (Apiocera) sp. #2	Australia	MEI 108213	AF266248
Apiocera (Pyrocera) haruspex	California	MEI 108214	AF266249
Apiocera (Pyrocera) sp. #3	Mexico	MEI 108197	AF266254
Family Mydidae			
Rhaphiomidas terminatus abdominalis	California	MEI 108215	AF266258
Megascelus albovillosus	Chile	MEI 108200	AF266250
Tongamya stuckenbergi	Namibia	MEI 089484	AF266259
Diochlistus hackeri	Australia	MEI 108192	AF266251
Rhopalia sp.	Israel	MEI 108194	AF266253
Mitrodetus australis-group	Argentina	MEI 108198	AF266256
Neomydas pantherinus	Oregon	MEI 108195	AF266255
Arenomydas callosus	South Africa	MEI 108193	AF266257

Sequences were obtained by dye terminator cycle sequencing using the ABI Taq FS enzyme (PE Applied Biosystems, Foster City CA), gel fractionated, and base-called on the ABI PRISM™ 377 DNA sequencer (PE Applied Biosystems, Foster City CA). Opposite strands were confirmed for all templates. ABI trace files were edited and contigs assembled using the program GAP4 in the STADEN software package (Staden 1996) on a SUN Ultra1 workstation. The final nucleotide alignment is available from the European Molecular Biology Laboratory Nucleotide Alignment Database (EMBL 2000) or as a website-based, downloadable alignment file (Wiegmann 2000).

Alignments were constructed manually using the multiple alignment editor of the Genetic Data Environment (GDE 2.2) (Smith *et al.* 1994). Positions within the 28S divergent domains for which alternative *ad hoc* placement of indels could affect the phylogenetic outcome were excluded from the analysis. Boundaries of excluded regions were set by inspection as the last position whose alignment preserves unambiguous adjacent positional homology. Gaps were treated as missing data. Phylogenetic trees were constructed using equally-weighted parsimony methods in PAUP*4b2a (Swofford 1999). Heuristic searches were performed using 100 replicate random addition searches with tree bisection-reconnection (TBR) branch swapping. Bremer support values (Bremer 1988 1994) were calculated by heuristic search (TBR) with 10 replicates of random additions using TreeRot v.2 (Sorenson 1999). Bootstrap support values (Felsenstein 1985) were obtained from 500 replicate resampled data sets and heuristic searches (TBR). Maximum likelihood (ML) analyses were performed in PAUP*4b2a using the following likelihood parameter settings: HKY85 6-parameter model of nucleotide substitution, empirical base frequencies, transition/transversion ratio set to 2:1, and assuming substitution rates follow a gamma distribution with shape parameter equal to 0.5 (Yang 1994). These same parameters were used to carry out 100 replicate ML bootstrap searches conducted in PAUP*4b2a.

Specimens used in molecular analysis and specimens other than *Tongamya* referred to in this paper

Specimens used in the molecular component of this study (both outgroup and ingroup) and those, other than *Tongamya*, used in the morphological component of this study are listed below, alphabetically arranged by genus, conforming to the specimen examined format (see above). The collection where the parts of the insect not used in the molecular analysis are housed is the listed repository. Genus and species are given in full with author and date of publication in the section that follows. All parts used for the molecular analyses are with NCSU (Brian Wiegmann's laboratory). GenBank numbers are provided in Table 1.

Apioceridae

Apiocera (*Apiocera*) sp. 1 (Apioceridae). AUSTRALIA, Queensland, Carnarvon National Park, Tombs, [-25.0886°, +147.8667°], along rock wall, 29-XI-1997 to 2-XII-1997, Malaise trap, J. H. Skevington, C. Lambkin, 1 male (*MEI 108212*, NCSU).

Apiocera (*Apiocera*) sp. 2. AUSTRALIA, Queensland, Mount Walsh National Park, Mount Walsh Summit, [-25.5733°, +152.0514°], 3-XII-1998, hand netted, C. Lambkin, D. K. Yeates, C. J. Burwell, 1 female (*MEI 108213*, NCSU).

Apiocera (*Anypenus*) *philippii* Brethes, 1924. CHILE, Quillota Province, Parque Nacional de Campanas, Palma de Ocoa, [-32.9324°, -71.0781°], in hillside draw, 215 m, 20-XII-1997 to 10-I-1998, Malaise trap, G. Barria, M. E. Irwin, 1 female (*MEI 108205*, MEIC).

Apiocera (*Pyrocera*) *haruspex* Osten Sacken, 1877. MEXICO, Baja California Norte, Río San Salvador at Highway 3, [+31.8733°, -116.0908°], 1067 m, 12-VI-1997, hand netted, M. E. Irwin, E. I. Schlinger, 1 male (*MEI 108214*, NCSU).

Apiocera (*Pyrocera*) sp. 3. MEXICO, Baja California Norte, Río San Salvador at Highway 3, [+31.8733°, -116.0908°], at flowing creek, 1067 m, 12-VI-1997, hand netted, M. E. Irwin, E. I. Schlinger, 1 female (*MEI 108197*, MEIC).

Mydidae: Megascelinae

Megascelus albovillosus Artigas, 1973. CHILE, Limarí Province, Fray Jorge National Park, Quebrada las Vacas, [-30.6448°, -71.6572°], on river bank, 190 m, 30-IX-1997 to 4-X-1997, Malaise trap, M. E. Irwin, D. K. Yeates, 1 male (*MEI 108200*, MEIC). Fray Jorge National Park, near park entrance gate [-30.6325°, -71.6104°], on trail, 335 m, 30-IX-1997, hand netted, M. E. Irwin, D. K. Yeates, 1 male (*MEI 108216*, MEIC), 1 female (*MEI 106333*, MEIC). Fray Jorge National Park, El Mineral, [-30.6571°, -71.6657°], in wet creek bed, 225 m, 4-XI-1997 to 10-XI-1997, Malaise trap, M. E. Irwin, H. Vasques, 1 male (*MEI 116793*, MEIC).

Megascelus nigricornis Philippi, 1865. CHILE, Malleco Province, Angol, [-37.8000°, -72.7167°], 10-XII-1959, hand netted, E. Aravena, 1 female (*MEI 116024*, MEIC).

Neorhaphiomidas hardyi Norris, 1936. AUSTRALIA, Western Australia, 1 km E. Yanchep Beach, [-31.5500°, +115.6167°], vegetated dunes, 5-XI-1987, hand netted, M. E. Irwin, E. I. Schlinger, 2 males (*MEI 118403*, *MEI 118404*, MEIC), 2 females (*MEI 118405*, *MEI 118406*, MEIC).

Tongamya stuckenbergi Irwin & Wiegmann, sp. n. NAMIBIA, Otjinene District, 2 km S Otjisume Farm [-21.3117°, +19.3222°], 1400 m, 27-XI-1996, hand netted, M. E. Irwin, 1 male (*MEI 089484*, MEIC).

Mydidae (other than the Megascelinae)

Arenomydas callosus Wiedemann, 1828. SOUTH AFRICA, Western Cape, Bokbaai, 15 km W Atlantis, [-33.5792°, +18.3125°], coastal vegetated dunes, 29-X-1996, hand netted, M. E. Irwin, 1 male (*MEI 108193*, MEIC).

Diochlistus hackeri Paramonov, 1950. AUSTRALIA, Queensland, Carnarvon National Park, Mt. Moffatt Section, Kenniffs Cave, [-24.8739°, +148.0219°], sandy highland, sclerophyll eucalyptus forest, 840 m, 23-XI-1995, hand netted, M. E. Irwin, 1 male (*MEI 108192*, MEIC).

Mitrodetus australis-group. ARGENTINA, La Rioja Province, Depart. de General La Madrid, 2 km N Villa Catelli, km 244 Hwy 26, [-28.9977°, -68.2027°], *Prosopis* covered dunes, 1292 m, 13-X-1997 to 15-X-1997, Malaise trap, M. E. Irwin, F. D. Parker, S. Roig, 1 female (*MEI 108198*, MEIC).

Neomydas pantherinus (Gerstäcker, 1868). USA, Oregon, Wasco County, 11.3 km E. The Dalles, along Hwy I-84, [+45.6436°, -121.0700°], sand dunes, 7-VII-1999, hand netted, M. E. Irwin, 1 male (*MEI 108195*, MEIC).

Rhaphiomidas terminatus abdominalis Cazier, 1941. USA, California, San Bernardino County, Colton, Delhi sand dunes, [+34.0739°, -117.3128°], VIII-1992, hand netted, G. Ballmer, 1 female (*MEI 108215*, NCSU).

Rhopalia sp. ISRAEL, Iddan, Arava Valley, [+30.7822°, +35.2442°], in small wadi, 28-IV-1996, hand netted, M. E. Irwin, 1 female (*MEI 108194*, MEIC).

Scenopinidae

Stenomphrale teutankhameni (Kröber, 1924). ISRAEL, Nizzanim Beach, [+31.7368°, +34.6148°], stable coastal dunes, 43 m, 15-IV-1995, hand netted, M. E. Irwin, 1 female (*MEI 029578*, NCSU).

Therevidae

Anabarhynchus tristis Bigot, 1890. AUSTRALIA, New South Wales, Warrumbungle National Park, Warrumbungle Mountains, at Wambelong Creek, [-31.2667°, +148.9500°], in cedar forest, at water hole in drying creek, 18-XII-1995, hand netted, M. E. Irwin, 1 female (*MEI 053735*, MEIC).

Ruppellia basalis (Loew, 1858). NAMIBIA, Windhoek District, Khomas Region, oasis at Gaub River, [-23.4867°, +15.7689°], riparian vegetation, 730 m, 22-XI-1996, hand netted, M. E. Irwin, 1 female (*MEI 089480*, NCSU).

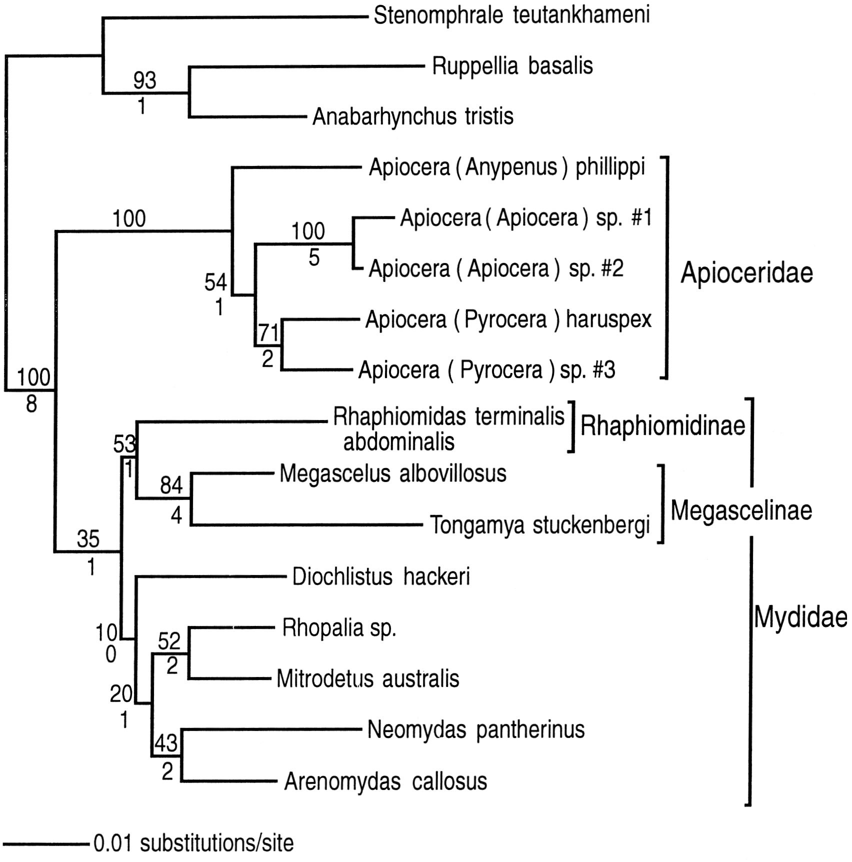


Fig. 1. Maximum likelihood tree based on 28S rDNA data.

RESULTS AND DISCUSSION

Phylogenetic Study

The 28S rDNA phylogenetic dataset comprised 1101 aligned bases of which 175 bases were variable and 83 were phylogenetically informative characters. Uncorrected pairwise sequence divergence ranged from 5–8% between outgroup and ingroup taxa (Table 1), and 2.5–5.5% between genera of Mydidae or Apioceridae (genus *Apiocera*). Phylogenetic analysis of the 28S rDNA data yielded the maximum likelihood tree shown in Figure 1 (-ln L=3332.55). Parsimony analysis supports an identical tree (not shown), differing only in the resolution of the placement of the Australian mydid, *Diochlistus hackeri* (length = 310; RI= 0.67; CI= 0.72). The maximum likelihood topology (Fig. 1) is only one step longer than the most parsimonious tree, and the two alternative trees are statistically indistinguishable by Templeton's (1983) test for topological congruence (p= 0.5637; Johnson & Soltis 1998).

Both parsimony and maximum likelihood results show low support for relationships among the mydid species sampled from several continents. Among these groups, only

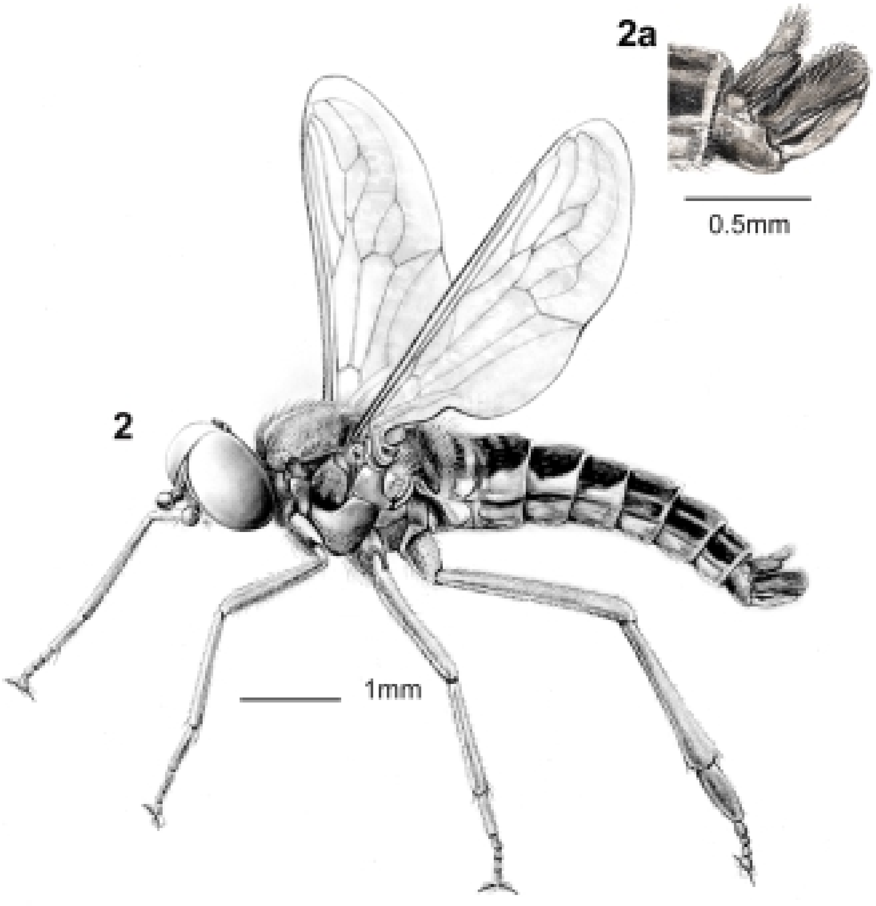


Fig. 2. Habitus view of male *Tongamya stuckenbergi* sp. n. (*MEI 109134*). 2a. Magnified view of male terminalia, lateral view.

the close relationship of *Megascelus* and *Tongamya* is strongly supported by the molecular data (84% bootstrap support, 4 steps Bremer support). Strong support is also shown for the monophyly of the Apioceridae + Mydidae, the monophyly of the Apioceridae, and the basal position of the Rhaphiomydinae and Megascelinae relative to all other Mydidae.

The molecular data are largely concordant with the higher-level morphological hypothesis of relationships proposed by Yeates & Irwin (1996). Our molecular phylogenetic analysis was largely aimed at testing the morphologically based position of *Tongamya* hypothesised by Yeates & Irwin (1996). The 28S rDNA evidence presented here confirms the sister group relationship of *Tongamya* and *Megascelus* (no properly preserved specimens were available of the Australian genus *Neorhaphiomidas* to test its position within the Megascelinae by molecular analysis), their removal from Apioceridae, and their classification as a subfamily (Megascelinae) of Mydidae. The DNA-based tree differs from the morphologically based topology only in placing the Rhaphiomydinae as sister to the Megascelinae, but this position is not strongly supported by bootstrap (53%) or Bremer support (1) values. Morphological data (Yeates & Irwin 1996) place Rhaphiomydinae as the basal mydid lineage, as it lacks key synapomorphies that would unite it with megascelines + higher mydids. Unfortunately, taxa sampled for the morphological analysis were not available as fresh preserved tissue for molecular work, allowing little overlap of taxa of Apioceridae and Mydidae between the two studies. The generally low sequence variability found among sampled mydid genera suggests that the 28S rDNA may have limited resolving power within the family. Increased sampling of both genes and morphology for a larger and more complementary dataset will further improve the encouraging, but not yet fully comparable, evidence from these two preliminary phylogenetic studies.

Systematics of *Tongamya*

Genus *Tongamya* Stuckenberg

Tongamya Stuckenberg, 1966: 110.

Type species: *Tongamya miranda* Stuckenberg, by original designation.

miranda Stuckenberg, 1966: 112. Holotype locality: South Africa, Tongaland, Ingwavuma District, Ndumu Game Reserve rest camp (*ca.* 32° 17' E, 26° 55' S), 290 ft above sea level. Collected at light trap on 1–4 December 1963 by B. R. & P. J. Stuckenberg. Holotype male (No. 1093) in the Natal Museum, Pietermaritzburg, South Africa (NMSA).

stuckenbergi Irwin & Wiegmann, sp. n. Holotype locality: Namibia, Otjinene District, 2 km S. Otijsume Farm (21° 18' 42" S, 19° 19' 19" E), 1400 meters above sea level (Fig. 4). Collected on 27 November 1996 by M. E. Irwin. Holotype male (*MEI 109134*) deposited in the Namibian National Insect Collection, Windhoek, Namibia (SMWN).

Diagnosis of Tongamya *as a genus within the Megascelinae*: The genus *Tongamya* has the following characteristics that separate it from other genera of the Megascelinae. In general, head and mesonotal pile of *Tongamya* shorter and less dense than that of *Megascelus* and *Neorhaphiomidas*. *Tongamya* is the only genus within the Megascelinae in which the anterior and posterior tentorial arms form two distinct, bilateral, tubular cavities that traverse the subcranium from front to back (see Peterson 1916: 30, for description of this phenomenon in *Mydas clavatus* (Drury)). Compound eyes of *Tongamya* males holoptic and divided into two regions with facets of different sizes (Figs 5, 6), while those of *Megascelus* and *Neorhaphiomidas* dichoptic with a single facet size. Mouthparts of *Tongamya* vestigial and non-functional, while they are

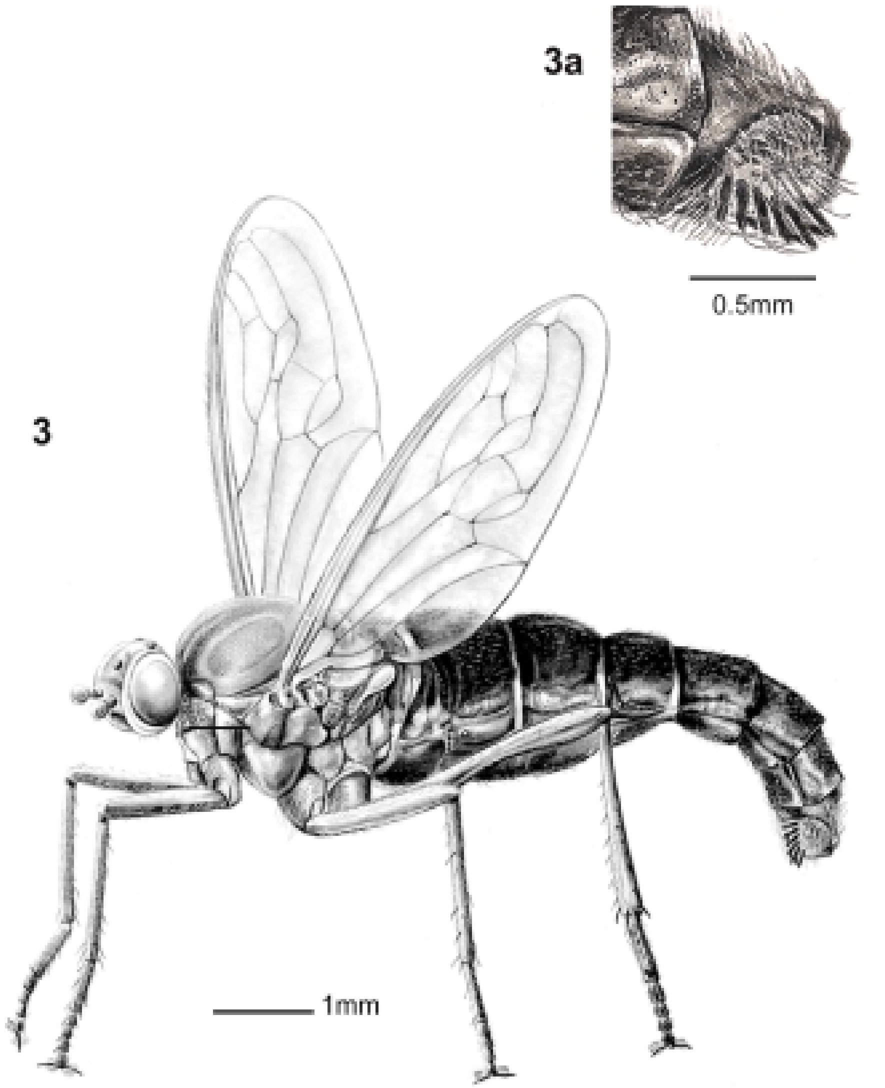


Fig. 3. Habitus view of female *Tongamya stuckenbergi* sp. n. (*MEI 109135*). 3a. Magnified view of female terminalia, lateral view.

considerably larger and functional in other megascelines. Anterior ocellus of all genera widely separated from posterior ocelli. Anterior ocellus of male *Tongamya* (and to a lesser extent those of female *Tongamya* and both sexes of *Neorhaphiomidas*) unusually large, while that of both sexes of *Megascelus* much smaller, approaching size of posterior ocelli. Spiracles of abdominal segment 1 large and conspicuous in *Tongamya*; in the other megascelines they are not detectable. Hind basitarsus of male somewhat shortened and greatly swollen in *Tongamya* (Fig. 2) (we suggest that the swelling of these parts in *Tongamya* may function as a way to better grasp females while hovering in flight); in other megascelines hind basitarsus slender and elongate.

Male terminalia: Tergite 8 of *Megascelus* membranous, while those of *Neorhaphiomidas* and *Tongamya* heavily sclerotised anterodorsally. Epandrium of *Tongamya* (Figs 19, 21) and *Neorhaphiomidas* (Fig. 17) not extending posteriorly beyond apex of cercus and hypoproct, while that of *Megascelus* (Fig. 15) does. Gonocoxites of *Megascelus* and *Neorhaphiomidas* relatively short, extending posteriorly less than 1.5 times length of epandrium, while those of *Tongamya* extend more than 2.0 times length of epandrium (Fig. 14). Ventral plate of gonopod and hypandrium distinct sclerites in all three genera; in *Megascelus* (Fig. 16) and *Neorhaphiomidas* (Fig. 18) separation demarcated by very weak sclerotisation, while in *Tongamya* (Figs 20, 22) this union demarcated by heavily sclerotised, strap-like posterior section of the hypandrium (Figs 18, 20). In *Megascelus* gonocoxites solidly fused along anterodorsolateral plane to apex of dorsal aedeagal apodeme, while in *Neorhaphiomidas* gonocoxites only slightly united, and in *Tongamya* not united with aedeagus. Ejaculatory apodeme larger in *Megascelus*, lying in a groove formed by the ventral apodeme of the aedeagus (Figs 23, 24), smaller in *Neorhaphiomidas*, projecting only slightly anterior to and 'suspended' above ventral apodeme (Figs 25, 26), while in *Tongamya* ejaculatory apodeme considerably smaller and positioned within groove of ventral apodeme (Figs 27–30). In *Neorhaphiomidas* union between anterior end of hypoproct and anterodorsal end of aedeagal dorsal apodeme lateral, not medial, and rigid; in both *Tongamya* and *Megascelus,* union is medial, hinge-like, and weak. Cerci and hypoproct of *Megascelus* narrow and elongate (Fig. 15); those of *Tongamya* (Figs 19, 21) and *Neorhaphiomidas* (Fig. 17) broader.

Female terminalia: Megasceline genera *Tongamya* and *Megascelus* have two large, weakly sclerotised spermathecae (note that Artigas (1970, Fig. 37) illustrated *Megascelus nigricornis* Philippi as having three spermathecae; in our dissections of a female of that species (*MEI 116024*), only two were present). *Neorhaphiomidas* apparently has single weakly sclerotised spermatheca (upon dissection of terminalia of both female specimens of *Neorhaphiomidas hardyi* in our possession, a single spermatheca was discovered in each; a second spermatheca might not have been uncovered during these dissections). Spermathecae of *Tongamya* (Fig. 32) and *Megascelus* (Fig. 33) subovate; those of *Neorhaphiomidas* (Fig. 34) spherical. All three genera have medial, narrow and slightly twisted, elongate spermathecal sacs (Winterton *et al.* 1999). Spermathecal sac of *Tongamya* elongately swollen and cone-shaped (Fig. 32), that of *Neorhaphiomidas* semi-coiled and pointed apically (Fig. 34), and that of *Megascelus* elongate and sac-like (Fig. 33). Common duct of spermathecae plus spermathecal sac short in *Megascelus*, somewhat longer in *Tongamya*, and very long in *Neorhaphiomidas*. Independent duct of the spermathecal sac of *Tongamya* (Fig. 32) and *Neorhaphiomidas* (Fig. 34) rather short, while that of *Megascelus* (Fig. 33) relatively longer. Acanthophorites of all three genera bearing 6–11 thick, blunt, digging spines (Fig. 35). Cerci of female *Tongamya* (Fig. 35) and *Neorhaphiomidas* sausage-shaped and relatively large, while those of *Megascelus* more spherical and smaller.

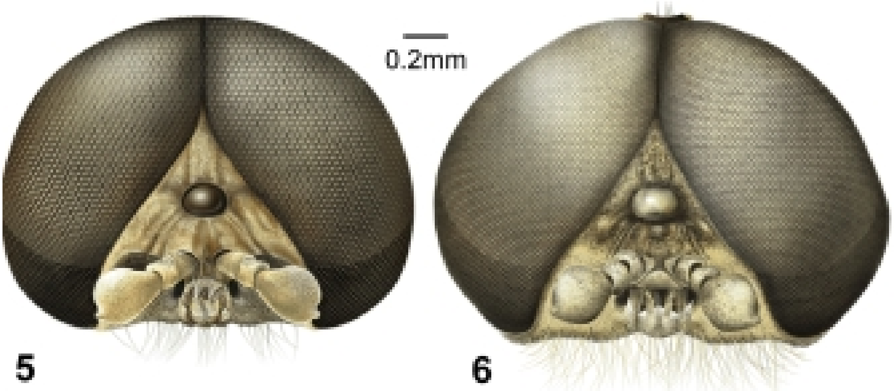
Proposed synapomorphies for species within the genus *Tongamya*: Within the megasceline genera, species within *Tongamya* are characterised and grouped by the following set of proposed synapomorphies: (1) anterior and posterior tentorial arms form two distinct, bilateral cavities that are completely open and contained within the internal sclerotised tentorial arms, traversing the subcranium of adults of both sexes from front to back; (2) compound eyes of males holoptic and divided into larger upper and smaller lower facets; (3) mouthparts vestigial, appearing non-functional; (4) anterior ocellus of male extraordinarily large; (5) hind basitarsus of male greatly swollen; (6) aedeagus not attached to gonocoxites; (7) spermathecal sac distally cone-shaped; and (8) males hover in the air awaiting females.

Diagnoses of the species within *Tongamya*

Tongamya contained a single described species, *miranda*, until the discovery of a congener, *T. stuckenbergi* sp. n., which is described below. A number of features separate one from the other, the most apparent of which are discussed here. From the few specimens in hand, the body of *miranda* appears longer and the paler parts darker than those of *stuckenbergi*.

Head: Male head in lateral view wider above and narrows below; this difference more striking in *miranda* (Fig. 11) than *stuckenbergi* (Fig. 12), and less evident in females; compare *miranda* (Fig. 9) with *stuckenbergi* (Fig. 10). Upper portion of ocellar tubercle of male *stuckenbergi* (Fig. 6) visible when head viewed from anterior position (straight on), while that of *miranda* (Fig. 5) is not. Frons of male at outer lateral bases of anterior ocellus of *stuckenbergi* depressed into shallow, darkened concavities that extend laterally as depressions to compound eye margins (Fig. 6); in *miranda*, depressions lighter in colour, shallower in depth, broader in area, and set higher on frons at middle of outer lateral margins of anterior ocellus (Fig. 5). Frons of female *miranda* dark tan with prominent depression between anterior ocellus and antennae that is bordered laterally by a strong, horizontal ridge (Fig. 7), while frons of *stuckenbergi* pale tan with shallower depression and slightly less pronounced ridge across this area (Fig. 8). Facial area flattened and recessed, forming buccal depression, within which and located below and slightly laterad of each antenna, in *stuckenbergi* (Fig. 6) lies a laterally compressed, narrowly suboval, dark-walled aperture (the anterior tentorial pit) that passes through the head via the tentorial rods; while in *miranda* the aperture is more broadly suboval (Fig. 5). Antennal scape of *stuckenbergi* yellow with dorsal circlet of light brown setae and patch of brown ventral setae, while scape of *miranda* yellowish-brown, with shorter, darker brown setae. The two hind ocelli are situated at either end of a transverse, raised, log-shaped ridge (ocellar tubercle) at back of vertex; in male *stuckenbergi* this ridge considerably raised (Fig. 12), while in *miranda* it is not (Fig. 11). Maxillary palps are considerably reduced in both species; in *stuckenbergi* they are elongate and pointed, while in *miranda* they are compressed and shortened, conical lobes.

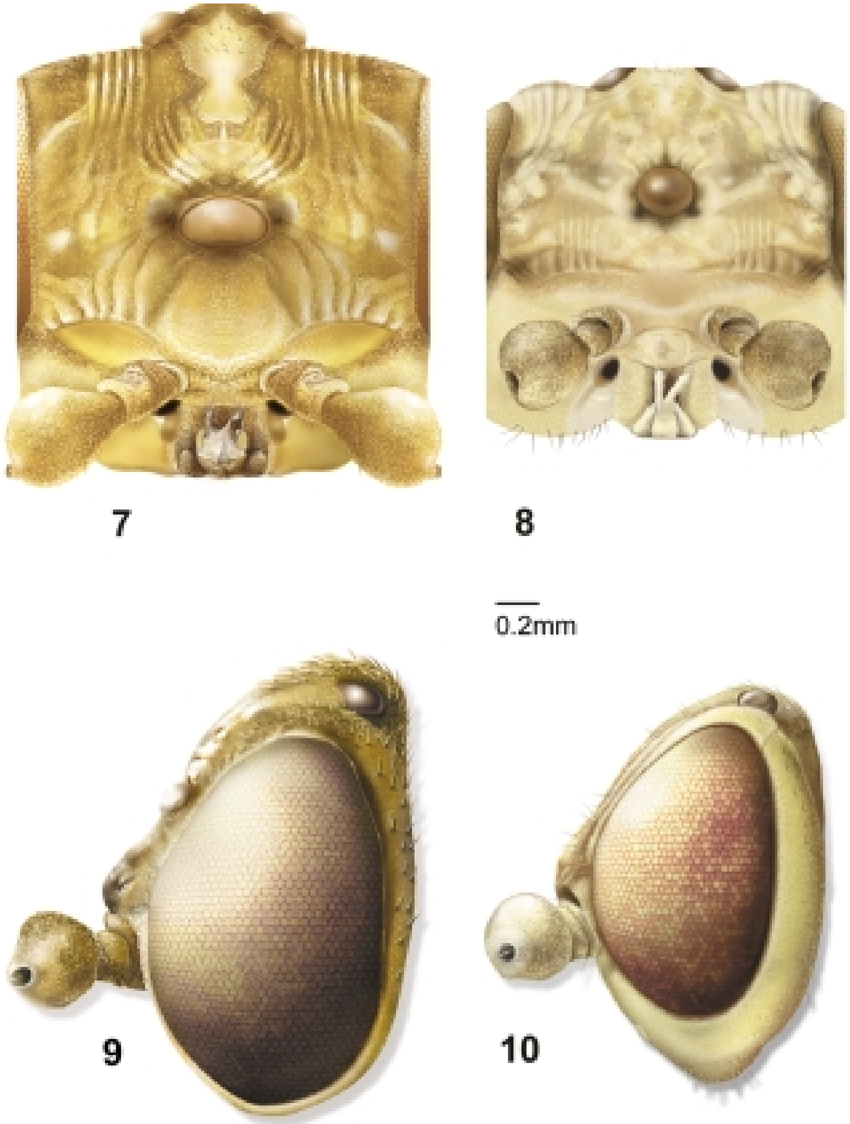
Thorax: The placement of the dark brown thoracic markings varies considerably between *stuckenbergi* and *miranda*, most notably, *stuckenbergi* does not have a marking at the midlateral edge of the mesonotum while *miranda* does. Legs of *stuckenbergi* have rather dense, short, recumbent, yellowish-tan hairs over all surfaces, including anteroventral setae of hind tibia, while those of *miranda* have similar hairs, many dark brown in colour, especially the anteroventral setae of hind tibia (Angola (*MEI 116621*) and Etosha (*MEI 108188*) specimens currently placed within *stuckenbergi* have pale yellow hairs, with rows of slightly darkened anteroventral setae on hind tibia). Halter of *stuckenbergi* has tan stem and white knob; that of *miranda* has darker brown stem and pale yellow to pale tan knob. In reflective light, wing membrane appears cloudy white in *stuckenbergi*



Figs 4–6. 4. Photograph of habitat where type material of *Tongamya stuckenbergi* sp. n. was collected (2 km S Otjisume Farm, Otjinene District, Namibia); note that the vegetation is not fully leafed. 5–6. Heads of male *Tongamya*, frontal views. 5. *T. miranda* Stuckenberg, 1966 (*MEI 116615*). 6. *T. stuckenbergi* sp. n. (*MEI 109134*).

(Angola female is clear translucent) and clear translucent in *miranda*. Vein CuA_1 curves anteriorly to join M_3, forming a closed, often short m_3 cell in *stuckenbergi* (this vein of Etosha female curves anteriorly and forms a longer m_3 cell), whereas CuA_1 ends free, well before the wing margin in *miranda*.

Male terminalia: The posterior portion of tergite 8 in *stuckenbergi* appears translucent,



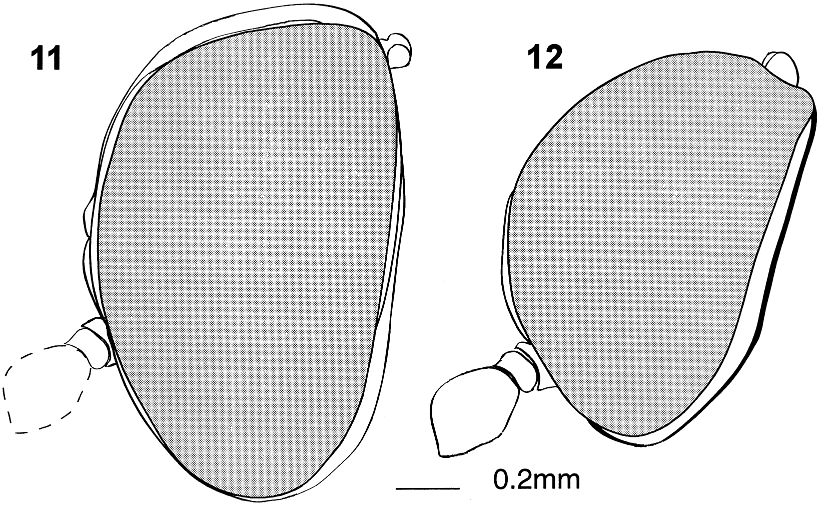
Figs 7–10. Heads of female *Tongamya*. 7–8. Frontal views, showing vertex, frons with anterior ocellus, antennae, face, and mouthparts. 9–10. Lateral views, showing vertex and ocellar tubercle, compound eye, frons, antennae, parafacials, genae, and occiput. 7, 9. *T. miranda* Stuckenberg, 1966 (*MEI 113930*). 8, 10. *T. stuckenbergi* (*MEI 109135*).

lacking pigmentation (Fig. 14), while that of *miranda* is more heavily pigmented. In *stuckenbergi* ventral plate of gonopod longer, flatter, and has broad apical excision extending basad for about one-fourth of its length (Fig. 22), while in *miranda*, this plate has narrow apical excision extending basad for about one-fifth of its length (Fig. 20). Undersurface of ventral plate broadly but shallowly channelled in *stuckenbergi* (Fig. 22), narrow and deep in *miranda* (Fig. 20). Aedeagal distiphallus of *stuckenbergi* narrow and flattened along its posterior third (Figs 29, 30), while distiphallus of *miranda* more uniformly cylindrical along its posterior third (Figs 27, 28). Ejaculatory apodeme of *stuckenbergi* small, its anterior end set at about the same level as anterior margin of aedeagal ventral apodeme (Figs 29, 30), while in *miranda* this structure extends forward past anterior margin of ventral apodeme (Figs 27, 28). Aedeagal lateral ejaculatory process of *stuckenbergi* horseshoe-shaped, the arms pointing dorsad, while in *miranda* the lateral ejaculatory process broadly circular, its dorsum forming a nearly united arch. Cleft between terminal lobes of cerci of *stuckenbergi* deep and narrowly 'V' shaped (Fig. 21), in *miranda* shallower and more 'U' shaped (Fig. 19).

Female terminalia: Both known species have similarly shaped female terminalia, although the hypoproct in *stuckenbergi* appears quite narrow and not as easily visible from the ventral view as that of *miranda*, which is larger and considerably broader.

Habitats associated with *Tongamya* adults: The two species of *Tongamya* inhabit somewhat similar 'bushveld' vegetation zones (Acocks 1988), albeit on different sides of the southern African subcontinent (Fig. 13). Both species are closely associated with thorny bush habitat overlying sandy substrates. *T. miranda* females were collected in several related vegetational zones: coastal forest and thornveld, Zululand thornveld, lowveld, and Mopani veld. The specimens MEI collected were on a flat outcropping of coarse, white sand with sparse vegetation comprised of small-leafed trees and thorny scrub. Perennial grass tufts (*Panicum* sp.) were scattered throughout the less vegetated fragments of this landscape, and females were observed within or near them (Irwin & Stuckenberg 1972). The type locality of *T. stuckenbergi* (Fig. 4) is within the Kalahari thornveld and, in particular, the thorn savanna dominated by *Acacia erioloba* E. May and *Acacia haematoxylon* Willd. (Acocks 1988). This vegetation zone is underlain with a deep, sandy substrate. The ground had no annuals at the time the flies were collected because the rains had only just begun. Although tuft grass is common to this zone, none was observed in the area where the specimens were captured.

Field observations of *Tongamya*: Female *T. miranda* flight, according to Irwin & Stuckenberg (1972), was slow, regular, and a bit unwieldy. The specimens seemingly crashed into grass stems without reducing their flight velocity. They used their somewhat expanded hind legs to hold onto the grass tufts. Only a single female of *T. stuckenbergi* (*MEI 109135*) was observed in the field. This specimen did not fly; instead she slowly walked around the base of a medium-sized shrub, which appeared to belong to the genus *Acacia* (the shrub was only beginning to leaf out and was difficult to identify). Her walk was irregular, staccato-like, and consisting of repeated forays into the base of the shrub followed by retreats. We assume the female was searching out appropriate oviposition sites. The original type series, all males, was collected at a mercury vapour light in early evening; a single male specimen was swept from foliage of a small tree, and Stuckenberg (1966) suspected from this, that the species was arboreal. Three males of *T. stuckenbergi* were observed in flight, but never more than two males were seen airborne and in the same vicinity at any time. In each case, the male was hand-netted while hovering at a height of about 3 meters above ground level in an open area bordered by medium-sized *Acacia* trees (Fig. 4). After a brief period of hovering and slowly drifting forward, then backward, which lasted less than 2 minutes, one of the males alighted close to the hover zone, about 1.5 meters above ground level,



Figs 11–12. Head profiles (lateral views) of male *Tongamya*. 11. *T. miranda* Stuckenberg, 1966 (*MEI 116615*). 12. *T. stuckenbergi* sp. n. (*MEI 109134*).

near the tip of a leafless stem of one of these shrubs. This hovering behaviour gives credence to the hypothesis that males with compound eyes of two facet sizes capture females in flight prior to copulation (Downes 1969). *Megascelus albovillosus* Artigas was observed in the field in north central Chile. Both males and females alighted on the ground, the males on small pebbles or sticks in sandy pathways. *Megascelus* males were not observed to hover, nor do they have divided eyes. Males and females of *Neorhaphiomidas hardyi* Norris were observed in the field in Western Australia by Evert I. Schlinger and MEI. Although males flew rapidly along open sandy pathways on vegetated dunes, apparently searching for flowers with nectar, none were observed to hover; they do not have divided eyes either. Females were also observed flying and were easier to follow than the males because their flight was more lumbered and less erratic.

Tongamya miranda Stuckenberg, 1966

Etiology: *mirandus* (L.), meaning wonderful, strange, singular. This species was named for its spectacular, unique morphology.

Type Material: Male holotype (No. 1093, NMSA) and four male paratypes from same locality (BMNH; MRAC; USNM; NMSA) [not examined]: SOUTH AFRICA, *KwaZulu-Natal*, Tongaland, Ingwavuma District, Ndumu Game Reserve, rest camp (*ca.* 32° 17' E, 26° 55' S), 290 ft above sea level, at light trap, 1–4 December 1963, coll. B. R. & P. J. Stuckenberg.

Distribution: The material at hand extends the originally reported range of this species from KwaZulu-Natal northward to the Kruger National Park, Northern Province, South Africa (Fig. 13).

Description: Refer to original description (Stuckenberg 1966) for description of male, and Irwin & Stuckenberg (1972) for description of female.

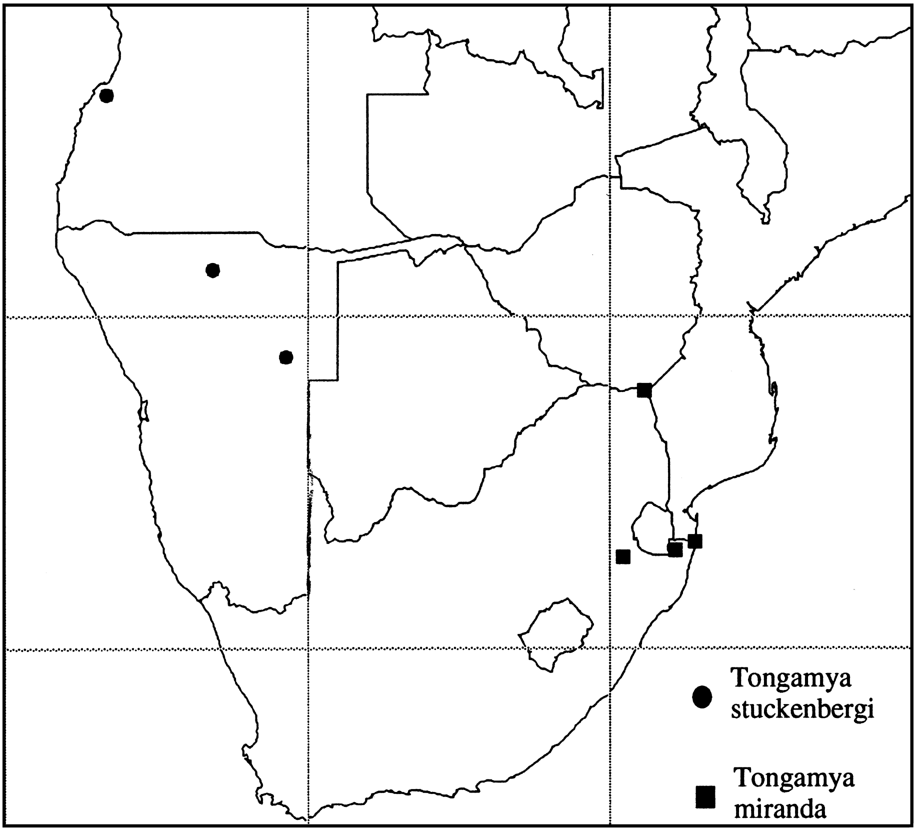


Fig. 13. Map of southern Africa depicting the known distribution of *Tongamya miranda* Stuckenberg, 1966 (squares) and *Tongamya stuckenbergi* sp. n. (circles).

Material Examined: SOUTH AFRICA, *KwaZulu-Natal*, 4 females, 32 km S. Ndumu Game Reserve camp [-27.2032°, +32.2481°], 29-XI-1971, hand netted, M. E. & B. J. Irwin, dry scrub forest, 100 m, (*MEI 109138*, MEIC; *MEI 116616*, SMWN; *MEI 116617*, NMSA; *MEI 113930*, NMNH); 3 males 1 female, Meseleni Mission Station [-27.3667°, +30.5167°], XII-1981, light trap, P. E. Reavell, (*MEI 116613*, MEIC; *MEI 116614*, NMSA; *MEI 116615*, NMSA; *MEI 116619*, NMSA); 2 females, Kosi Bay Nature Reserve [-26.9000°, +32.8667°], 30-XI-1982 to 2-XII-1982, J. G. H. Londt, D. Barraclough, B. R. Stuckenberg, open woodland, (*MEI 116618*, MEIC; *MEI 116620*, NMSA). *Northern Province*, 1 male, Kruger National Park, Nyandu Bush [-22.38°, +31.22°], 3-XII-1964, Kruger National Park Survey, L. Vári & J. Potgieter, (*MEI 109137*, TMSA).

Tongamya stuckenbergi Irwin & Wiegmann, sp. n.

Habitus illustrations of male (Fig. 2) and female (Fig. 3)

Etiology: This species is named for Brian R. Stuckenberg, mentor and life-long friend of MEI, in honour of a lifetime of meritorious contributions to African and World Dipterology.

Type Material: Male holotype (*MEI 109134*), two male paratypes (*MEI 109136*; *MEI*

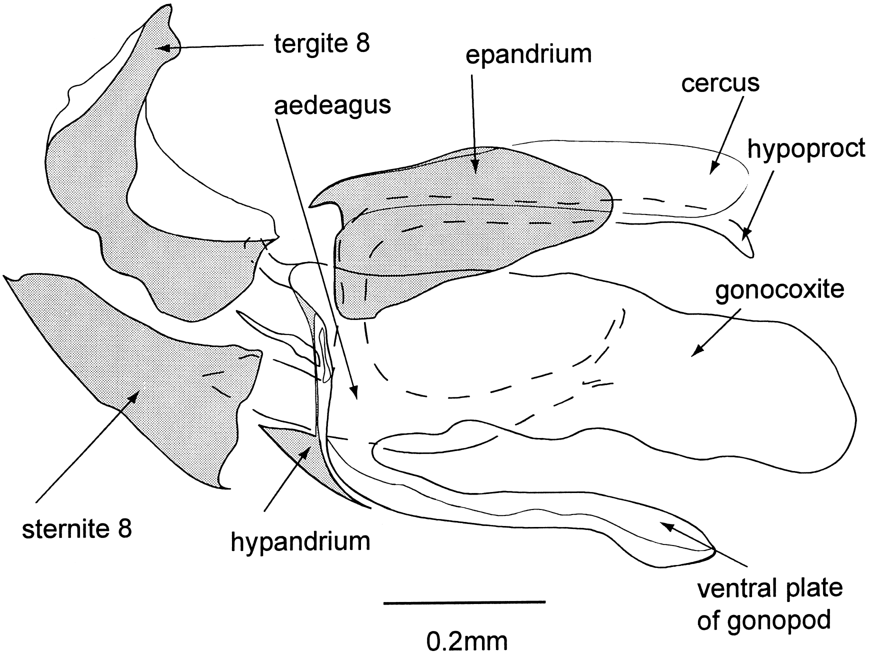


Fig. 14. Male terminalia, lateral view, of *Tongamya miranda* Stuckenberg, 1966 (*MEI 089484*) depicting tergite 8, sternite 8, and major sclerites of the genitalia.

089484), and one female paratype (*MEI 109135*) from the same locality and collection date (see material examined). The females from Angola (*MEI 116621*) and Etosha (*MEI 108188*) are included in the material examined below, but are not included as type material; upon discovery of males of these populations, they may prove to be a distinct species.

Distribution: The type material is from the westernmost edge of the Kalahari Desert in Namibia (Fig. 4). Two females that we currently place in this taxon are from northern Namibia (Etosha) and southwestern Angola (Fig. 13). (Note: Slight morphological differences separate the two female specimens (Angola and Namibia) from the material at the type locality. These two females extend the range delimited by the type material considerably northward; the differences between the type population and that of the northern specimens are discussed above (see 'Diagnoses of the species within *Tongamya*'). Males of these northern populations are unknown.)

Material Examined: ANGOLA, *Ambundos Province*, Benguela District, 1 female, 48 km S. Benguela [-13.0113°, +13.4039°], 21-IV-1971, H. D. Brown, (*MEI 116621*, NMSA). NAMIBIA, 1 female, Etosha National Park, Mushara [-18.6167°, +16.8833°], 14-X-1986 to 15-XI-1986, E. Griffin, (*MEI 108188*, SMWN); 3 males 1 female, Otjinene District, 2 km S. Otjisume Farm [-21.3117, +19.3222], 27-XI-1996, hand netted, M. E. Irwin, 1400 m, (*MEI 109134* [holotype], SMWN; *MEI 109136* [paratype], NMSA; *MEI 089484* [paratype] [thorax macerated for DNA], NCSU, [remainder of specimen], MEIC; *MEI 109135* [paratype], NMSA).

Description: The following description is, for the most part, based on the holotype male (*MEI 109134*). The internal male terminalia are described from a dissected male paratype

(*MEI 089484*). Where appropriate within the description, morphological variation based on the other male paratype (*MEI 109136*) is provided. The single topotypical female specimen (*MEI 109135*) is described below the male description; comparisons are made with the two more northern females (*MEI 108188* and *MEI 116621*), tentatively placed within this taxon.

Male (Fig. 2): Body length, excluding antennae, 11.0 mm (*MEI 109134*); 11.4 mm (*MEI 109136*).

Head: Head large (Figs 2, 6), wider above, narrowing below (Fig. 12). Ocellar tubercle visible in frontal view (Fig. 6), formed by a transversely raised, rounded ridge. Frons narrowly triangular (Fig. 6). Pruinescence light yellowish-grey overall. Antennae short, attached at lower third of head (Fig. 10); ratio of scape:pedicel:flagellum, 4:2:9. Apex of flagellum subpyriform with off-centered fovea; stylus one-segmented. Compound eyes occupying most of head (Fig. 12); eye facets divided at level of antennae; lower facets smaller (Fig. 6). Anterior ocellus enlarged; posterior ocelli one-third as broad and far removed from anterior ocellus (Fig. 6). Occiput with short, scattered, outwardly radiating pale blond setae. Mouthparts greatly reduced; medially placed labium directed upward, cleft apically, forming a pair of elongate labial palps. Elongate, thinly pointed, spine-like structure, formed by union of two robust, convergent setae, directed outward and upward. Small, one-segmented maxillary palp flanking lateral edges of prementum.

Thorax: Tanish yellow, including legs with well defined dark brown patches on upper portion of antepronotum, outer lateral edges of basisternum, flanking anteriomesal edge of postalar callus, lateral edges of scutellum, anterolateral margins of postnotum, anteroventral portion of anepisternum, outer portion of anterior basalare, ventral most axillary sclerite, anterior and posterior edges of sclerite supporting anterior spiracle, anterior half of subalar sclerite, anterior edge of sclerite supporting posterior spiracle, lower half of both katepisternum and meron, anterobasal and apical margins of fore- and middle coxae, anterolateral face of hind coxa, dorso-apical tips of hind femora, and apical tarsomeres of all legs. Fine, sparse, tan pile confined to pronotum, outer lateral half of basisternum, and anterior face of forecoxa. Pile in a broad lateral sweep from postpronotal lobe to attachment of wing; parallel, longitudinal vitae of slightly shorter pile along flanks of mesonotum. Postpronotal lobes enlarged, tanish-yellow, with thin dusting of tan pruinescence and thin, dense, pale tan hairs. Presternum bare, with deep, ventro-medial groove. Scutellum deep, strongly transverse, yellow; dorsally flattened, mottled with tan pruinescence. Mesopleuron bare except pruinescence on ventral halves of katepisternum and meron, posterodorsal thirds of katepimeron, katatergite, outer lateral half of basisternum, and anterior face of middle coxa. Halter 1.4 mm in length; stem tan, knob white.

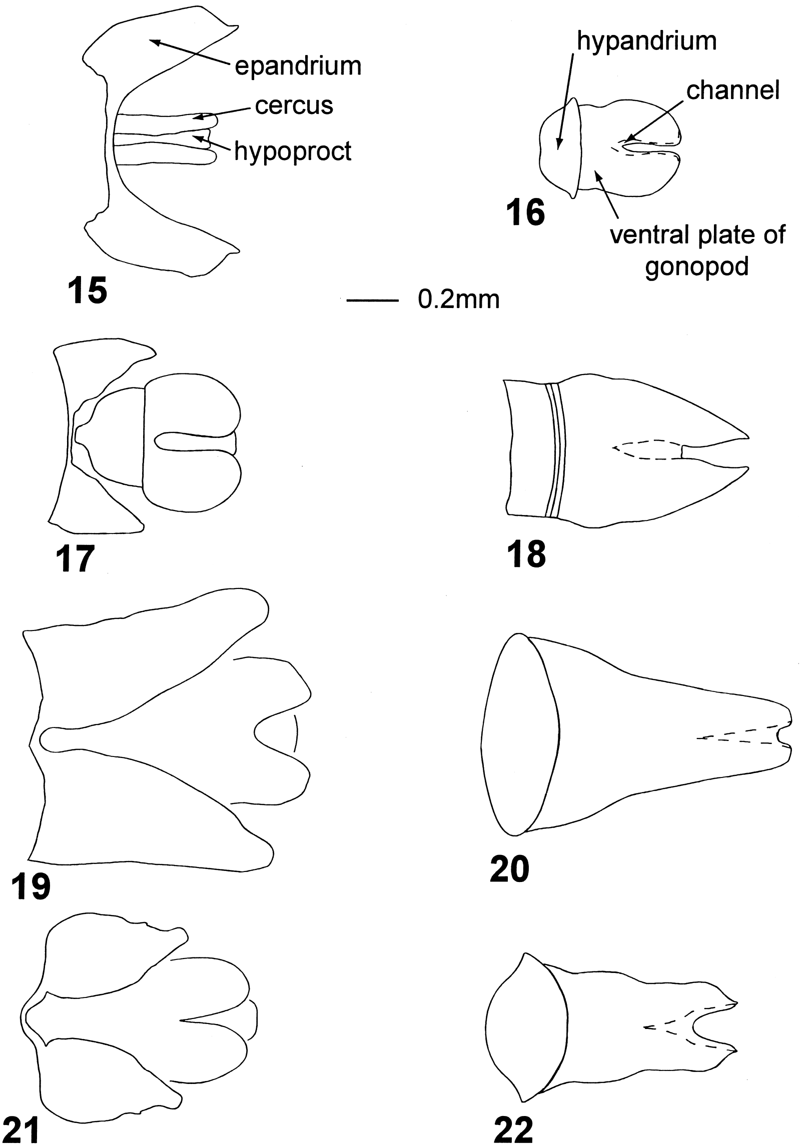
Wings (Figs 2, 3): Length 7.2 mm, of paratype 8.0 mm, 3 times longer than wide. Wing membrane transversely wrinkled, cloudy white; alula narrow. R_{2+3}, R_4 and R_5+M_{1+2} ending in R_1, joining R_1 almost at costa; CuA_2+M_3 curving upward to end in R_5+M_{1+2}.. Costa weakening gradually from base of junction with Sc to wing tip. Costa, subcosta, R_1, CuA_2 and, to a lesser extent, R_{2+3} and M_1 pale brown; remaining veins almost colourless. Vein CuA_1 curves upward to join M_3; m_3 cell closed.

Legs (Fig. 2): Surfaces of legs covered with dense, short, recumbent, yellow-tan hairs; hind tibial anteroventral setae short. Fore- and middle coxae with erect, sparse, yellow pile on anterior surface; hind coxa with similar pile on outer lateral surface. Hind legs conspicuously longer and thicker. Fore- and middle tibiae swollen apically; hind tibia greatly thickened apically, broadening to 2 times as wide at apex. Fore- and middle basitarsus thin, elongate, about 6 times longer than wide; hind basitarsus stout, about 2.5 times longer than wide, almost uniformly thick throughout, slightly narrower apically and almost as thick as apex of hind tibia.

Abdomen (Fig. 2): Elongate, tapering, 2.5 times longer than length of thorax. Tergite 1 swollen laterally, forming single broad, raised, tan callus across posterior half. Prominent circular spiracle imbedded within each posterodorsal corner of sternite 1. Spiracles of segments 3–7 set laterally in pleural membranes; sclerotised brown rings surround spiracular openings. Abdomen greasy in appearance, lacking pruinescence, with short, appressed, sparsely spaced pale yellow hairs, except for callus and terminalia, which have denser, longer hairs. T2–T7 dark, shiny brown dorsally, pale tan at lateral margins and as narrow wedges along outer posterior margins of T3–T7. Sternites and pleural areas pale tan; anteromedial portion of S2–S3 each with a small, dark brown, inverted 'V' marking, its arms coalesce into irregularly shaped blotches in similar positions on S4–S7.

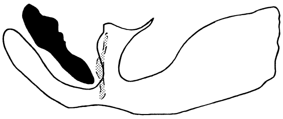
Male terminalia: Erect, yellow on preserved specimen. Tergite 8 (Fig. 14) lacking vestiture, arched, medially narrow, anteromesally heavily brown pigmented, posteromesally weakly pigmented. Sternite 8 broad, deep, shovel-shaped, weakly pigmented, without vestiture. Epandrium (Fig. 21) divided by broad median biconcave cleft into 2 subtriangular sclerites anteriorly connected by sclerotised strap; brown with thin, sparse, pale tan hairs over posteriodorsal four-fifths. Elongate, flattened, semi-forked plate (herein termed 'ventral plate of gonopod') lying beneath enlarged gonopod (Figs. 14, 22), heretofore assumed to be hypandrium in *Tongamya* (Stuckenberg 1966; Yeates & Irwin 1996) and *Megascelus* (Artigas 1970 1973). Our interpretation is that hypandrium may be a small, scoop-shaped, well sclerotised plate lying anterior to ventral plate of gonopod. If true, hypandrium bare, broadly scoop-shaped, overlapping ventral plate of gonopod (Fig. 22), supporting a pair of thin, strongly sclerotised arms that extend laterally and dorsally, and attach to lateral fold where gonopods and epandrium hinge (Fig. 14). Gonopod consisting of large, paired, robust gonocoxites (Fig. 14) and ventral plate of gonopod; gonostyli lost. Brown stripe along dorsolateral edge of each gonocoxite. Aedeagus consists of a slightly upcurved tube, widely open anteriorly and posteriorly, with a strong, dorsocentral, vertically oriented, rigid extension to base of hypoproct (Figs 14, 29). Distiphallus narrowing and flattening along apical third, flaring somewhat at apex (Figs. 29, 30). Ejaculatory apodeme small (Fig. 29). Lateral ejaculatory process (Sinclair *et al.* 1993) prominent, horseshoe shaped. Cerci form a shallowly roofed, bilobed sclerite (Fig. 21). Hypoproct horizontally flattened, thin, extending to apex of cerci (Fig. 14). Basally, hypoproct curves ventrad, uniting solidly with dorsocentral portion of aedeagus.

Female (*MEI 109135*): Length, excluding antennae, 15.8 mm. Similar to male but larger. Head proportionally smaller, 1.5 times wider than high. In lateral view, head narrow above, widest at level of antennae, narrowing below (Fig. 10). Frons wider than high, shallowly concave, with patchy, sparse, greyish-white pruinescence around anterior ocellus; with numerous, vertically oriented, subparallel, irregular grooves over frons and vertex (Fig. 8).



Figs 15–22. Sclerites of the male genitalia. 15, 17, 19, 21. Epandria, cerci, and hypoprocts, dorsal view. 16, 18, 20, 22. Hypandria and ventral plates of gonopods, ventral view. 15, 16. *Megascelus albovillosus* Artigas, 1973 (*MEI 108216*). 17, 18. *Neorhaphiomidas hardyi* Norris, 1936 (*MEI 118404*). 19, 20. *Tongamya miranda* Stuckenberg, 1966 (*MEI 116615*). 21, 22. *Tongamya stuckenbergi* sp. n. (*MEI 089484*).

Vertex yellow-tan with vertical swelling laterally (Fig. 8) (area between ocellar tubercle and compound eye of Etosha and Angola specimens not swollen); vertex elevated on sides above eye margins, forming a central, raised, tan ocellar tubercle (more prominent in Etosha and Angola specimens). Genae slightly swollen, cream-white, with thin white pruinescence. Compound eyes dichoptic, bare, small, undivided; facets uniform in size (Fig.10). Anterior



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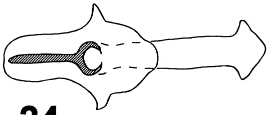

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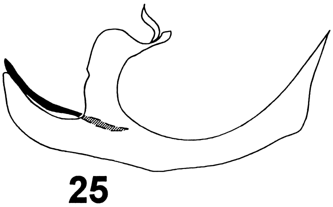

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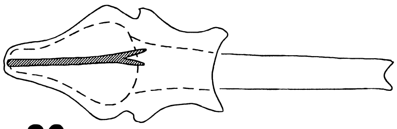

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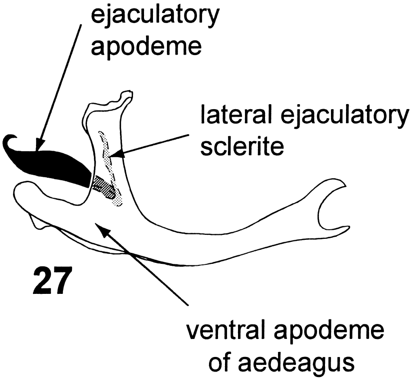

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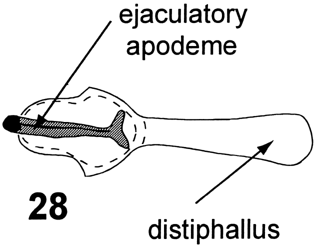

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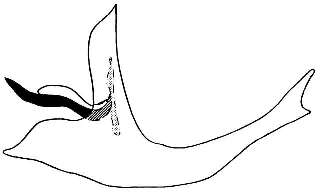

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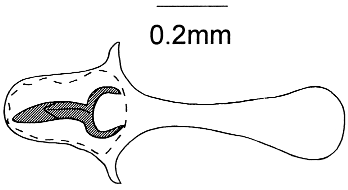

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Figs 23–30. Sclerites of the male genitalia. 23, 25, 27, 29. Aedeagus, lateral view. 24, 26, 28, 30. Aedeagus, dorsal view. 23, 24. *Megascelus albovillosus* Artigas, 1973 (*MEI 108216*). 25, 26. *Neorhaphiomidas hardyi* Norris, 1936 (*MEI 118403*). 27, 28. *Tongamya miranda* Stuckenberg, 1966 (*MEI 116615*). 29, 30. *Tongamya stuckenbergi* sp. n. (*MEI 089484*).

ocellus enlarged. Posterior ocelli smaller, situated laterally on ocellar tubercle, visible in frontal view (Fig. 8). Wing length 7.8 mm, width 2.6 mm. Hind tibiae and basitarsi not swollen (Fig. 3). Abdomen greasy in appearance, dark reddish-brown; swollen over first five segments (widest at segment 3), tapering rapidly at segment 6, with segments 7, 8 and genitalia cylindrical and half as thick as segment 3 (Fig. 3); white marking on posterolateral corners of T2–T4 (Fig. 3).

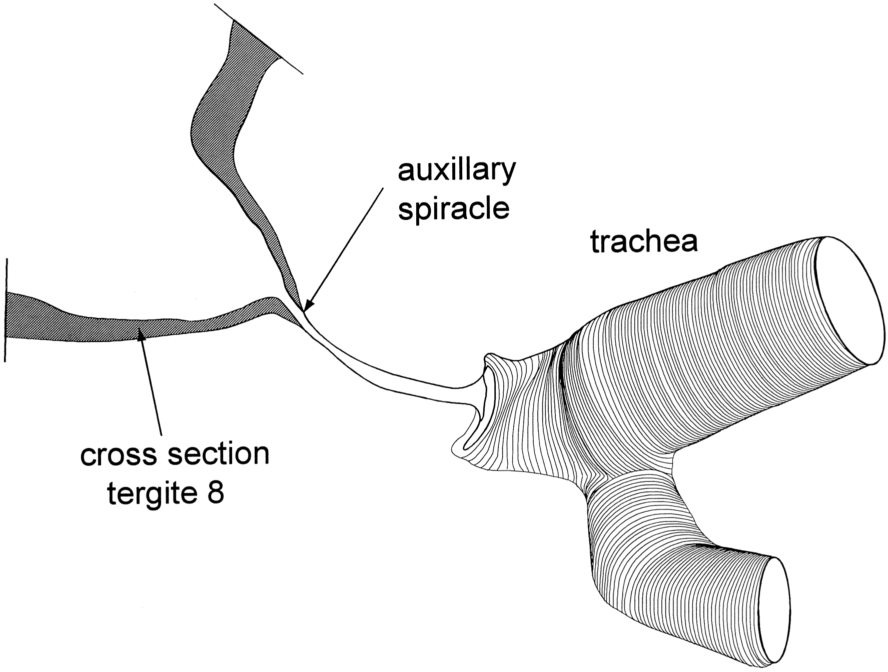

Fig. 31. Auxiliary spiracle of female tergite 8 in *Tongamya stuckenbergi* sp. n. (*MEI 108188*), showing cross section of tergite 8, the invaginated spiracular opening, and some larger internal tracheae. Orientation: the anterior end of the insect is to the left.

Female terminalia: Segment 8 telescoped within segment 7. Spiracles inset at weakly pigmented posterior area of segment 8; spiracular opening smaller than spiracles of other segments; characterised by thin trachea extending inward for a considerable distance, then expanding greatly within segment (Fig. 31) (termed ‘auxiliary spiracle’ by McAlpine *et al.* 1981). Tergite 8 (T8) elongate, ‘U’ shaped in cross section, tapering to shovel-shaped towards apex. Anterodorsal third relatively smooth and bare; rest of dorsum with short, sparse hairs. Sternite 8 (S8) similar in shape to T8 but shorter, narrower, ventrally smooth in texture with scattered, short, erect hairs. Posteriorly truncate, slightly infolded, forming shallow invagination. Tergite 9+10 (T9+10) heavily sclerotised, comprised of upper, anterior component (T9) and two ventrolateral, posterior sclerites (acanthophorites, T10) (Figs 32, 35). T9 dome-shaped (Fig. 35), divided into 2 narrowly fused dorsolateral sclerites (Fig. 32). Sternite 9 (furca, S9) (Fig. 32) framed by longitudinal, opposing, membrane-spanded struts. Spermathecal elements (Fig. 32) arise from gonopore as a common spermathecal duct. Two large, irregularly oval-shaped, weakly sclerotised spermathecae attach by thin spermathecal ducts to midpoint of common spermathecal duct, which extends as a twisted duct terminating in a spermathecal sac (Fig. 32) (Winterton *et al.* 1999). Two elongate, slightly bulging accessory glands attach by thin ducts originating from 2 minute, parallel apertures at posterior end of furcal membrane (Fig. 32). T10 (acanthophorites) (Figs 32, 35) paired sclerites, curving and widening ventrad, each baring circlet of 6–7 strong, flat, blunt spines (Fig. 35). Hypoproct at posterior margin of furca, extends posteromesally

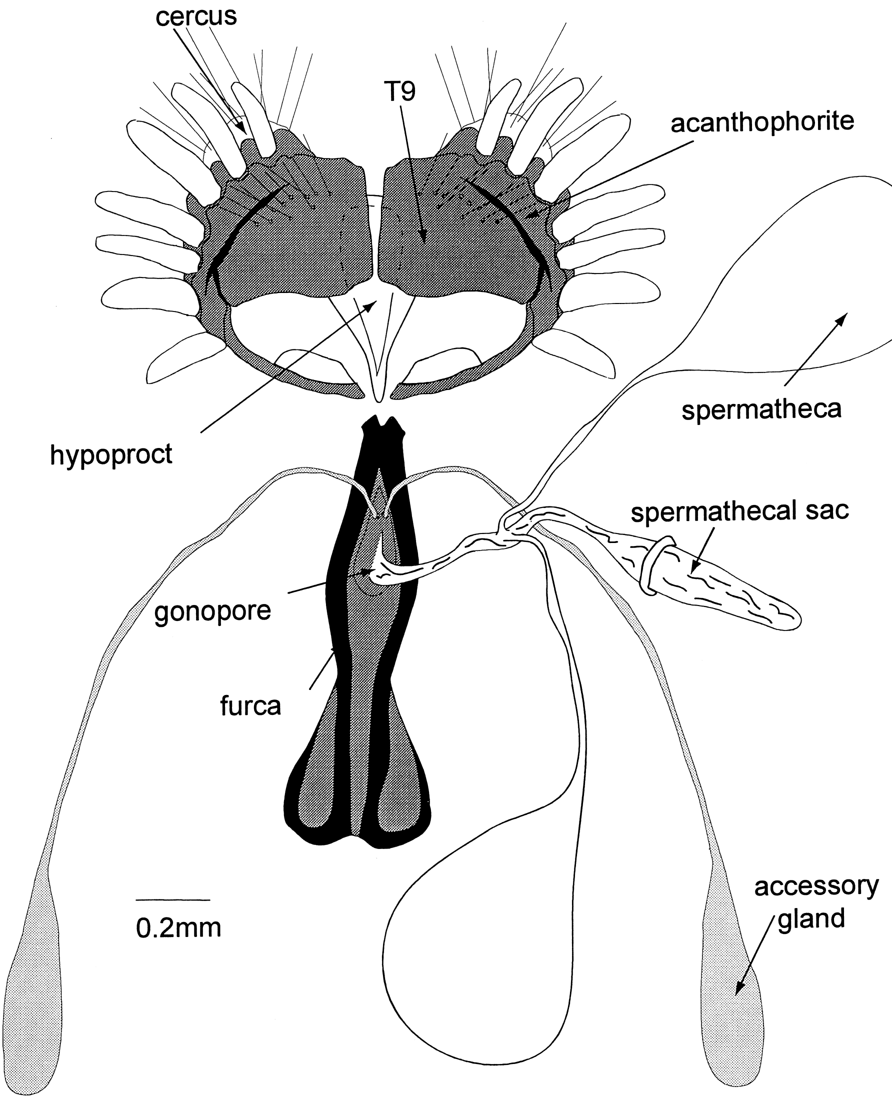

Fig. 32. Female genitalia of *Tongamya stuckenbergi* sp. n. (*MEI 108188*) depicting internal weakly sclerotised structures, dorsal view. T9 = tergite 9.

as a small, weakly sclerotised, long-haired structure, terminating between paired lateral cerci (Fig. 32). Cerci sausage-shaped, thinly sclerotised, longhaired, lying laterally within and conforming to inner basal curve of paired acanthophorites (Fig. 35).

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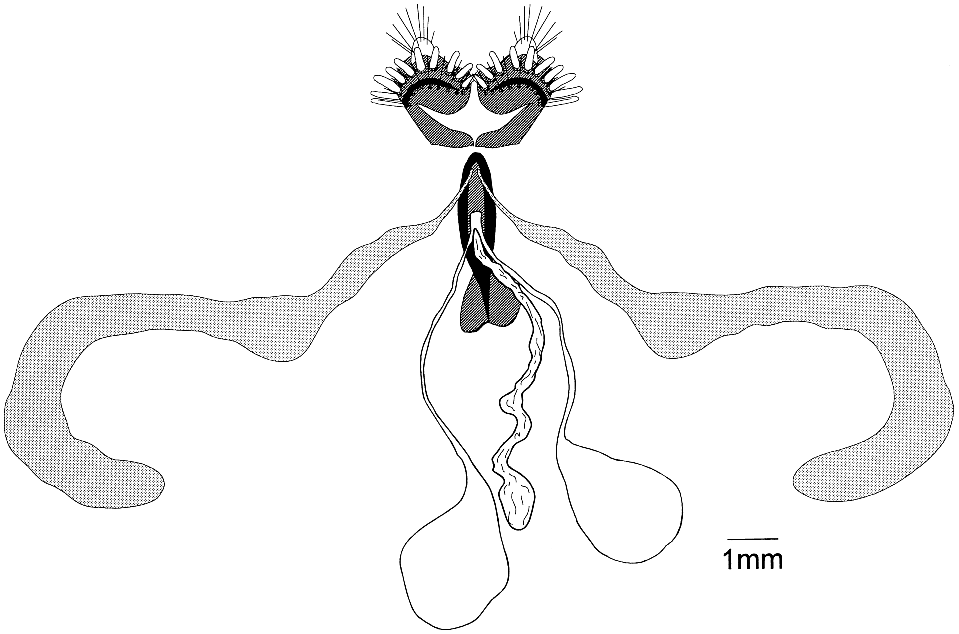

Fig. 33. Female genitalia of *Megascelus albovillosus* Artigas, 1973 (*MEI 106333*) showing internal weakly sclerotised structures, dorsal view (see Fig. 32 for names of parts).

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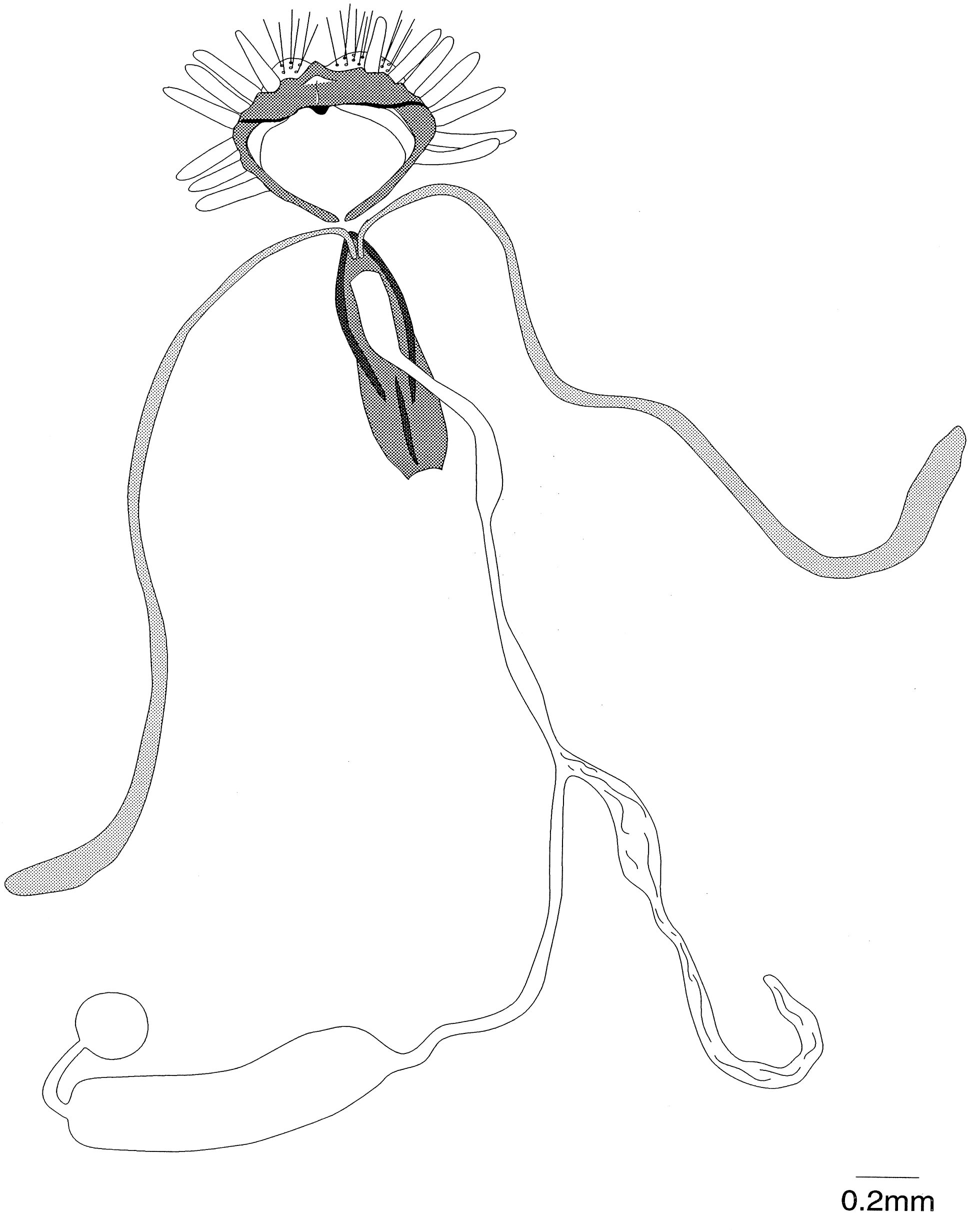

Fig. 34. Female genitalia of *Neorhaphiomidas hardyi* Norris, 1936 (*MEI 118406*) showing internal weakly sclerotised structures, dorsal view (see Fig. 32 for names of parts).

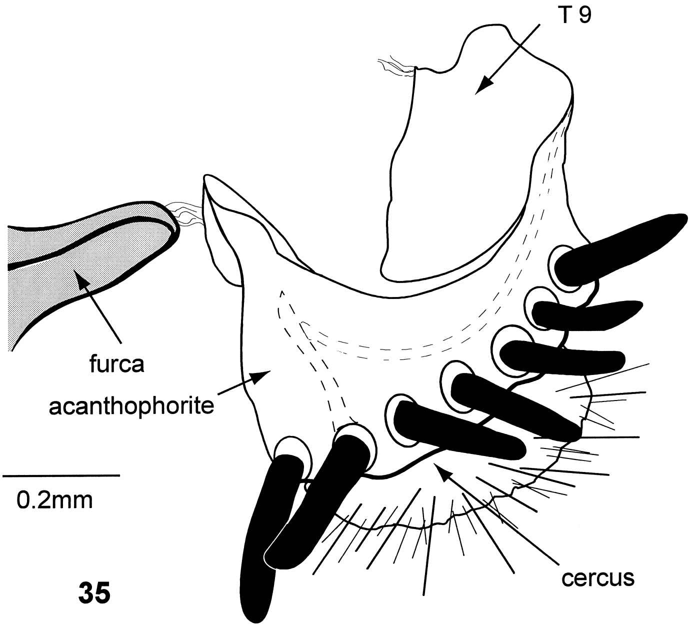

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Fig. 35. Female genitalia of *Tongamya stuckenbergi* sp. n. (*MEI 109135*), lateral view, depicting position of tergite 9 (T9), acanthophorite with digging spines, cercus, and anterior attachment to furca.

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